

TROPHIC STRUCTURE OF SOME NEARCTIC, NEOTROPICAL AND PALEARCTIC OWL ASSEMBLAGES: POTENTIAL ROLES OF DIET OPPORTUNISM, INTERSPECIFIC INTERFERENCE AND RESOURCE DEPRESSION

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ABSTRACT.—Trophic structure (i.e., food-niche relationships) of owls at levels of resolution ranging from entire predator assemblages to local populations were scrutinized. Results indicate that trophic structure changes geographically, that potentially competing owls vary in number and identity, and that owl trophic guilds usually include hawks and sometimes other carnivores. Analysis of trophic ecology of local populations of *Athene*, *Tyto* and *Bubo* owls living in Chile, Spain, California, and Colorado shows that diet breadths and mean prey sizes differ widely and inconsistently across regions. Apparently, varying characteristics of trophic structure emerge from opportunistic behavior of local owl populations with regard to profiles of prey size and abundance. Competition for food resources (when it occurs) may be more likely effected via resource depression rather than resource depletion, and the primary mechanism may be interference rather than exploitation.

Community ecology can be considered a shorthand term for studying the use sympatric organisms make of three major niche axes: habitat, time and food (Schoener 1974; Giller 1984). In the recent past segregation of sympatric species along niche axes was thought to be aimed at reducing exploitation competition by allowing potential competitors to gain access to different and exclusive food resources (MacArthur 1972; Cody 1974; Pianka 1983).

Community ecology studies on owls are still in their infancy (see Clark et al. 1978; Jaksic 1985). Probably because owl food habits are easier to study than habitat selection or activity time, most community-oriented studies have dealt with trophic structure (i.e., food-niche relationships) of sympatric owls. Considering those studies that deal with at least three sympatric species (the minimum number that I think qualifies as an assemblage of owls), an early, pioneering stage can be recognized between 1930–1970 (e.g., Cahn and Kemp 1930; Errington 1932; Wilson 1938; Uttendorfer 1939; Kirkpatrick and Conway 1947; Hagen 1952; Craighead and Craighead 1956; Weller et al. 1963; Ross 1969). During this stage, quantifications of prey consumed by sympatric owls were interpreted qualitatively without recourse to summary indices or statistical testing, and general conclusions were drawn with emphasis on “the balance of nature.”

A second stage began in the 1970s when the first modern ecological treatment of an owl assemblage was published by Marti (1974), followed by those of Herrera and Hiraldo (1976), Lundberg (1979),

Jaksic (1983), Mikkola (1983), Yalden (1985), and Korpimäki (1986b, 1987a), among others. The sophistication of quantitative and statistical testing of trophic relationships of sympatric owls varied but usually emphasized measures of diet similarity in light of competition theory, particularly those aspects bearing upon niche segregation, species packing and limiting similarity.

Despite increased quantification and regard for theory testing, little is known about the trophic structure of owl assemblages. A recurring theme, however, is that trade-offs between habitat and diet alleviate interspecific competition (e.g., Yalden 1985, following the tradition started by Lack 1946). Although sympatric owl species (e.g., those inhabiting the same forest) may differ in the use of different habitat categories (i.e., they may be allotopic, some in forest cores, others in forest gaps), it has yet to be shown that partitioning of the habitat axis actually leads to a reduction of overlap in use of prey resources (see Nilsson 1984, for the opposite finding). Exploitation competition is clearly not reduced if allotopic owls use the same habitat-generalist prey population. Regardless whether a prey population is used by different owl species in a forest patch or in an adjacent meadow, owl species may still be exploiting the same prey resource and competition may not be alleviated. The same applies to temporal segregation. Regardless whether a prey population is being exploited temporally by different owl species, the prey resource may still be one and the same (see Jaksic 1982; R. L. Knight, pers. comm., disagrees).

Although many factors may impinge upon the ecology of particular owl species (e.g., nest-site availability, Lundberg 1979), I think that understanding the organization of owl assemblages lies in how different sympatric owls use available prey resources; that is, in the study of the trophic structure of owl assemblages.

OBJECTIVES AND METHODS

I examined trophic structure of some Nearctic, Neotropical, and Palearctic owls by scrutinizing four levels of aggregation: the single owl population, the owl assemblage (>2 species), the raptor assemblage (owls and hawks), and the predator assemblage (owls, hawks, mammalian carnivores and snakes). Specific questions asked were: first, What is the trophic structure of owl assemblages (i.e., Do sympatric owl species segregate in their use of prey, or do they converge upon some particular prey, thus forming trophic guilds)? Second, What is the effect of including other sympatric predators in analyses of trophic structure (i.e., If trophic guilds exist are they composed solely of owls or include other predator types)? Third, Does trophic structure remain constant or change geographically? Fourth, If the latter is verified, what may be the underlying causes for changes in trophic structure?

With these questions in mind, I first examined quantitative information on the diet of sympatric (not necessarily syntopic) raptors in a number of localities in Nearctica: Michigan, Wisconsin and Utah; Neotropica: central Chile; and Palearctica: southern Spain. Published information (Errington 1932, 1933; Craighead and Craighead 1956; Valverde 1967; Smith and Murphy 1973; Jakšić et al. 1981) is based on analysis of regurgitated pellets (obtained mainly during the breeding season) including very detailed identification of their prey contents (to species level in the case of vertebrates). Based on such data, I constructed diet matrices and calculated all pairwise diet overlaps (i.e., diet similarities, using Pianka's 1973 formula) among sympatric species in all assemblages (see original data in Jakšić 1982). Diet matrices were subjected to UPGMA (Unweighted Pair Group Method with Arithmetic Average) clustering technique (Sneath and Sokal 1973) to obtain similarity dendrograms depicting trophic structure of each assemblage.

Secondly, I examined trophic structure of three predator assemblages (central Chile: Jakšić et al. 1981; southern Spain: Jakšić and Delibes 1987; central California: Jakšić, in prep.) for which the diets of all (or most) sympatric predatory vertebrates (i.e., owls, hawks, mammalian carnivores and snakes) were known. Thirdly, I reanalyzed results on geographic variation in trophic structure of European owl assemblages as documented by Herrera and Hiraldo (1976). Although Mikkola (1983) provides a more thorough data set (E. Korpimäki, pers. comm.), I found that Mikkola's results generally coincided with those of Herrera and Hiraldo (1976). Fourth, I summarized geographic variation of trophic metrics for owls of the genus *Athene* (Jakšić and Marti 1981), *Tyto* (Jakšić et al. 1982), and *Bubo* (Jakšić and Marti 1984). Trophic metrics summarized were diet breadth (or trophic diversity, using

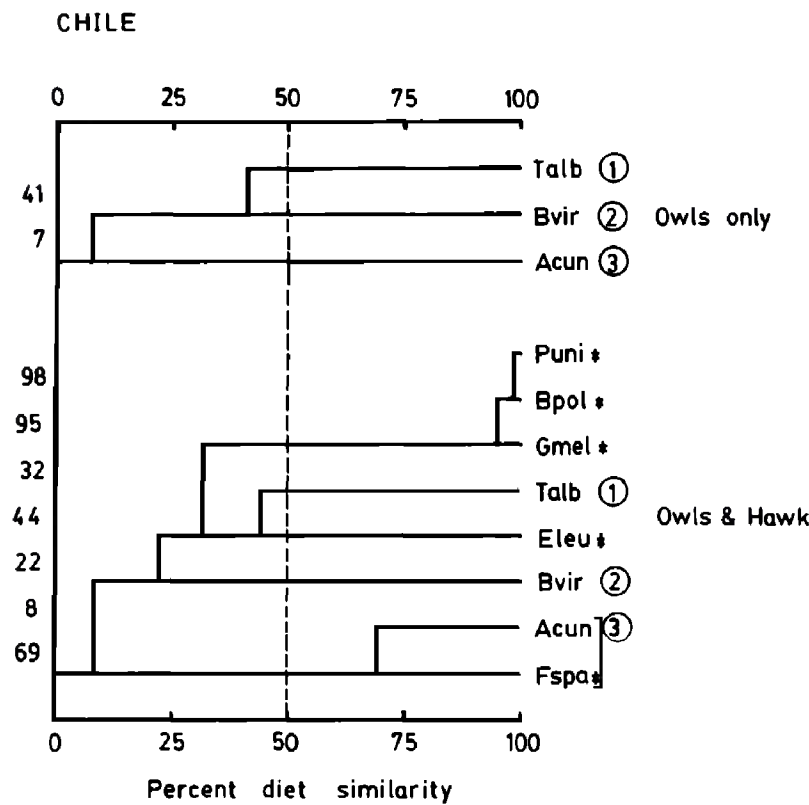
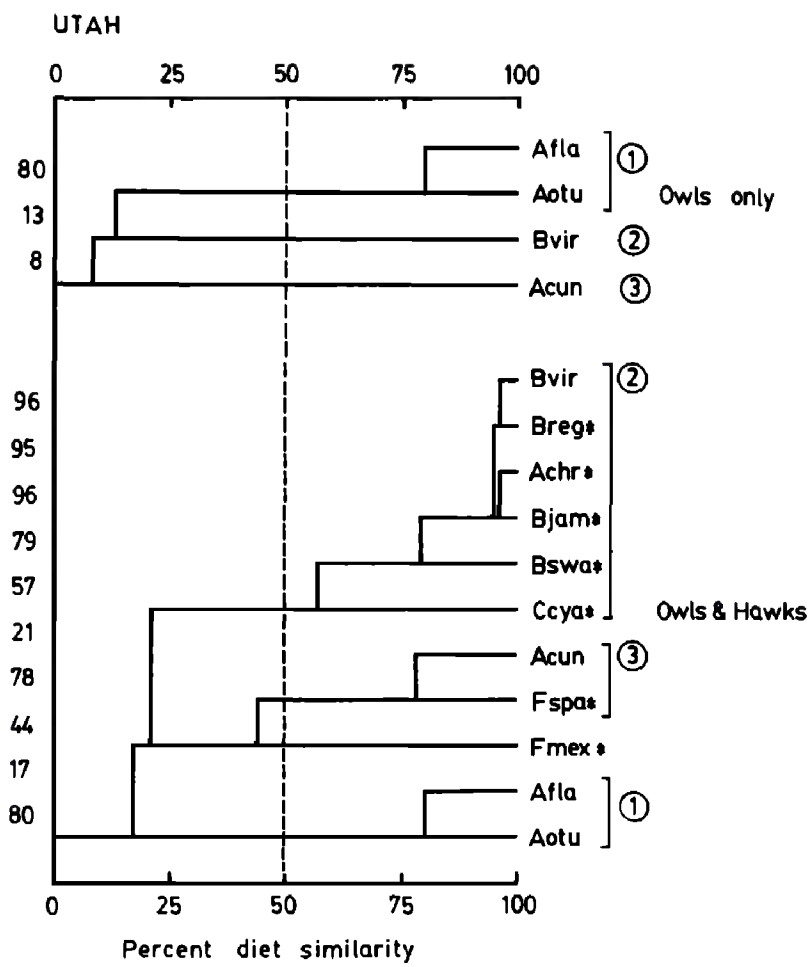
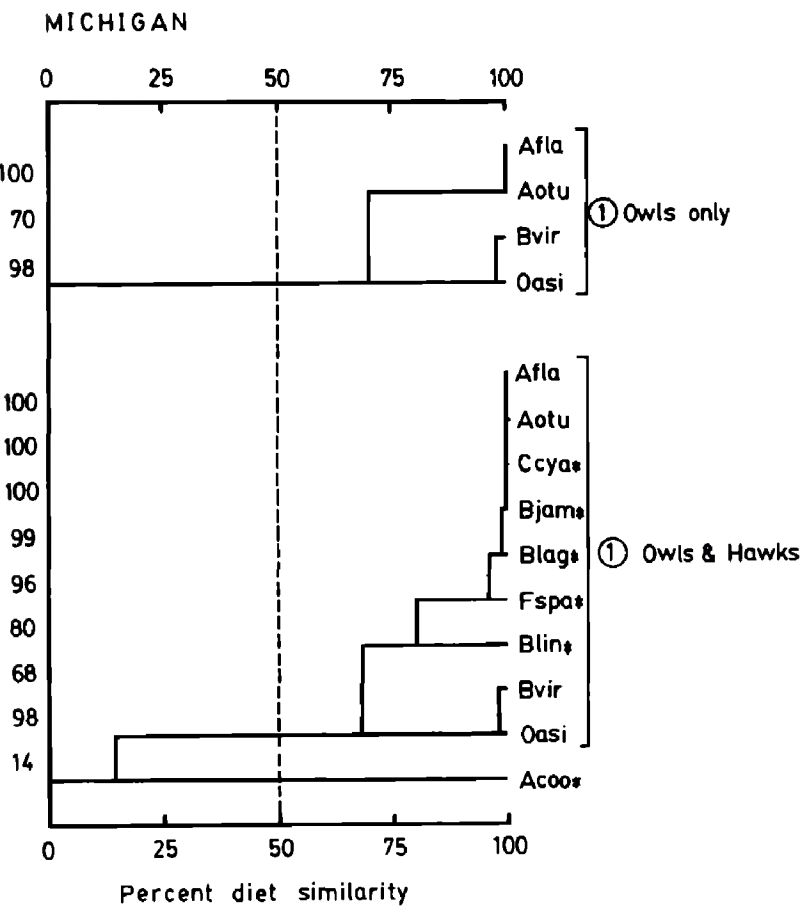
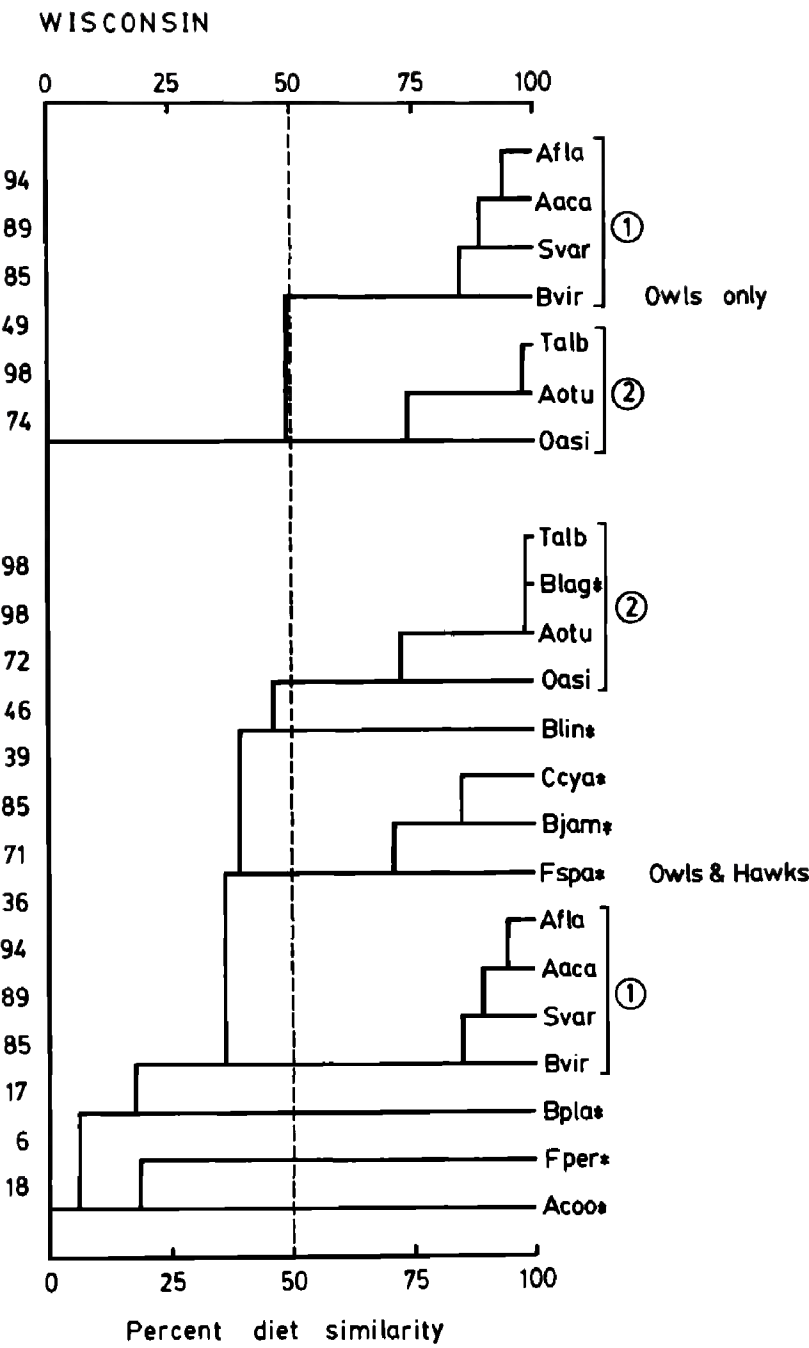
Herrera's 1974 formula), and arithmetic mean prey weight (see Jakšić and Marti 1981).

RESULTS

I first focus on trophic patterns shown by owls only before including sympatric hawks in a reanalysis of data sets. Using 50% diet similarity as an arbitrary minimum for assigning guild membership, two owl trophic guilds can be identified in Wisconsin (Fig. 1A). When sympatric hawks are included in the analysis, one owl guild expands to incorporate a hawk species. In Michigan (Fig. 1B) the owl assemblage is more tightly structured forming a single trophic guild, which increases greatly in size (from four to nine species) when sympatric hawks are included in the analysis. In Utah (Fig. 1C) a single guild is recognized at the owl assemblage level, but three become apparent after consideration of sympatric hawks. A similar situation is verified in Chile (Fig. 1D), where no trophic guilds made up solely by owls can be recognized, but at least one becomes formed by an owl and a hawk species. In Spain (Fig. 1E) a two-species owl guild increases in size to three when sympatric hawks are considered.

Interestingly, raptor trophic guilds are frequently composed of both nocturnal owls and diurnal hawks, a condition that attests to the inadequacy of temporal segregation as a mechanism to reduce the presumed exploitation competition for prey species active both day and night (Jakšić 1982; Carothers and Jakšić 1984; Korpimäki 1987b). Work in progress at the Snake River Birds of Prey Area (J. R. Parrish, pers. comm.), however, suggests that for that raptor assemblage time is indeed an orthogonal dimension that can be partitioned to reduce co-use of prey resources.

But predator assemblages are not only composed of owls and hawks. What happens when one analyzes the trophic structure of all sympatric predators (including mammalian carnivores and snakes) in a locality? In central Chile (Jakšić et al. 1981) there are 11 common predators. The trophic structure of the assemblage is very simple (Fig. 2A): two owls (*Tyto alba* and *Bubo virginianus*) appear to specialize on different prey and *Athene cunicularia* clusters with *Falco sparverius*. The situation in southern Spain is more complex (Jakšić and Delibes 1987), where 25 predator species form different trophic associations (Fig. 2B). Among owls, *Tyto alba* and *Strix aluco* cluster, and *Athene noctua* and *Otus scops* do so with a variety of other predators. Other members of this



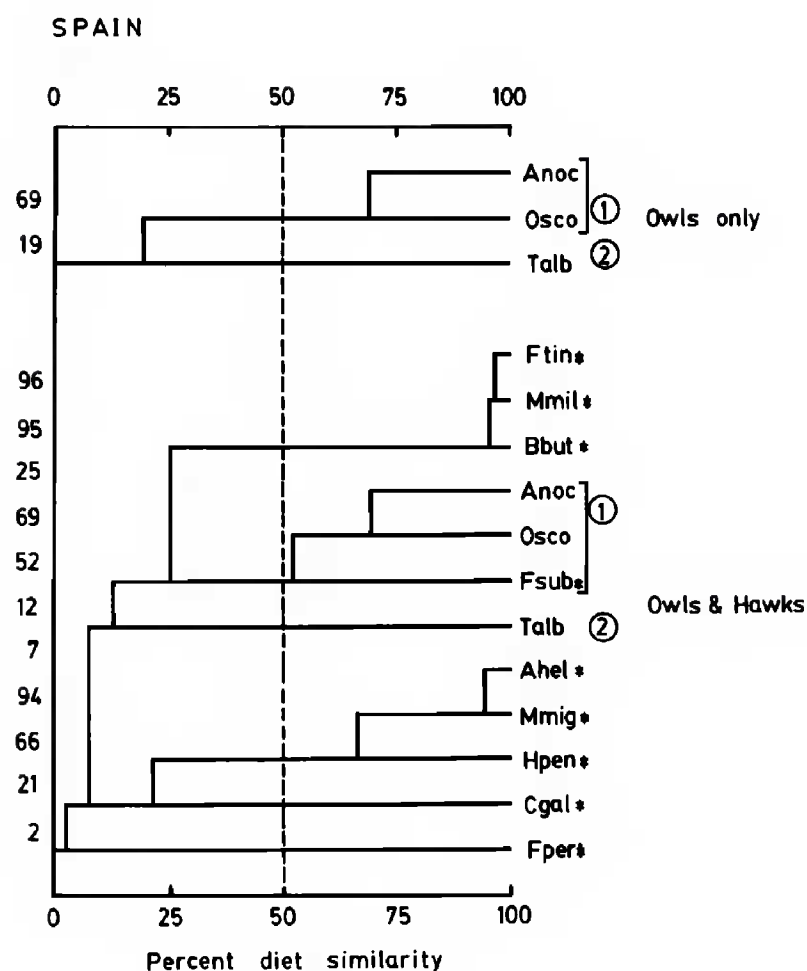


Figure 1. Trophic structure of owl and raptor assemblages in: A) Wisconsin, B) Michigan, C) Utah, D) Chile, and E) Spain. Using 50% diet similarity as the minimum to assign trophic guild membership, owl-only and owl-plus-hawk guilds are enclosed in brackets and assigned the same number for ease of identification. Names of owl species are as follows: Aaca = *Aegolius acadicus*, Acun = *Athene cunicularia*, Anoc = *Athene noctua*, Afla = *Asio flammeus*, Aotu = *Asio otus*, Bvir = *Bubo virginianus*, Oasi = *Otus asio*, Osco = *Otus scops*, Svar = *Strix varia*, Talb = *Tyto alba*. Names of hawk species (*) are: Achr = *Aquila chrysaetos*, Ahel = *Aquila heliaca*, Acoo = *Accipiter cooperii*, Bbut = *Buteo buteo*, Bjam = *Buteo jamaicensis*, Blag = *Buteo lagopus*, Blin = *Buteo lineatus*, Bpol = *Buteo polysoma*, Bpla = *Buteo platypterus*, Breg = *Buteo regalis*, Bswa = *Buteo swainsoni*, Ccya = *Circus cyaneus*, Cgal = *Circaetus gallicus*, Eleu = *Elanus leucurus*, Fmex = *Falco mexicanus*, Fper = *Falco peregrinus*, Fspa = *Falco sparverius*, Fsub = *Falco subbuteo*, Ftin = *Falco tinnunculus*, Gmel = *Geranoaetus melanoleucus*, Hpen = *Hieraaetus pennatus*, Mmig = *Milvus migrans*, Mmil = *Milvus milvus*, Puni = *Parabuteo unicinctus*.

large guild are the hawk *Falco subbuteo* and the carnivores *Genetta genetta*, *Meles meles*, *Vulpes vulpes* and *Herpestes ichneumon*. In central California (Jaksić, in prep.) 11 predator species show the following trophic structure (Fig. 2C): *Tyto alba* does not belong to a guild, but a very complex guild is formed by *Bubo virginianus* and the hawk *Buteo jamaicensis*, the carnivores *Canis latrans* and *Urocyon cinereoargenteus*, and the snake *Crotalus viridis*.

Trophic nearest neighbors within owl guilds change geographically not only in number but also in taxonomic identity. A reanalysis of trophic structure of European owls (Fig. 3) based on data originally reported by Herrera and Hiraldo (1976) shows that *Asio otus*, *Aegolius funereus* and *Bubo bubo* belong to three different guilds in northern Europe but to a single guild in central Europe. Also, *Athene noctua* does not belong to the guild composed by *Strix aluco* and others in central Europe, but both belong to the same guild in southern Spain. *Tyto alba* and *Bubo bubo* dissociate from *Strix aluco* in southern Europe (these results coincide with those of Mikkola 1983). Korpimäki (1987a) has shown that geographical changes in owl guild composition may occur over relatively short distances.

Two major conclusions can be drawn from evidence so far presented. First, owl-only trophic guilds appear to be a rare phenomenon; instead, owls' trophic nearest neighbors are usually hawks, sometimes mammalian carnivores and even snakes (see also Phelan and Robertson 1978; Bradley 1983; Erlinge et al. 1984; Korpimäki 1984, 1985a, 1985b, 1987b). Secondly, nearest neighbors in trophic space (i.e., potential competitors) vary in number and identity across geographical ranges (see also Jaksić 1983; Mikkola 1983; Korpimäki 1987a).

In an attempt to find causes for variation in guild structure of owl assemblages, Carlos Herrera, Carl Marti and myself have examined trophic ecology of populations of *Athene*, *Tyto* and *Bubo* owls living in Chile, Spain and California (Jaksić and Marti 1981; Jaksić et al. 1982; Jaksić and Marti 1984). The areas chosen have similar climate, physiognomy and vegetation (di Castri et al. 1981), and taxonomic and size composition of owl assemblages are also similar (Jaksić 1983). Colorado owls were also included as a non-mediterranean outgroup. Owls present in these four localities are *Athene cunicularia* in Chile, *Athene cunicularia* in both California and Colorado and *Athene noctua* in Spain. *Tyto alba* is present in all four localities. *Bubo* owls are represented by *Bubo virginianus*.

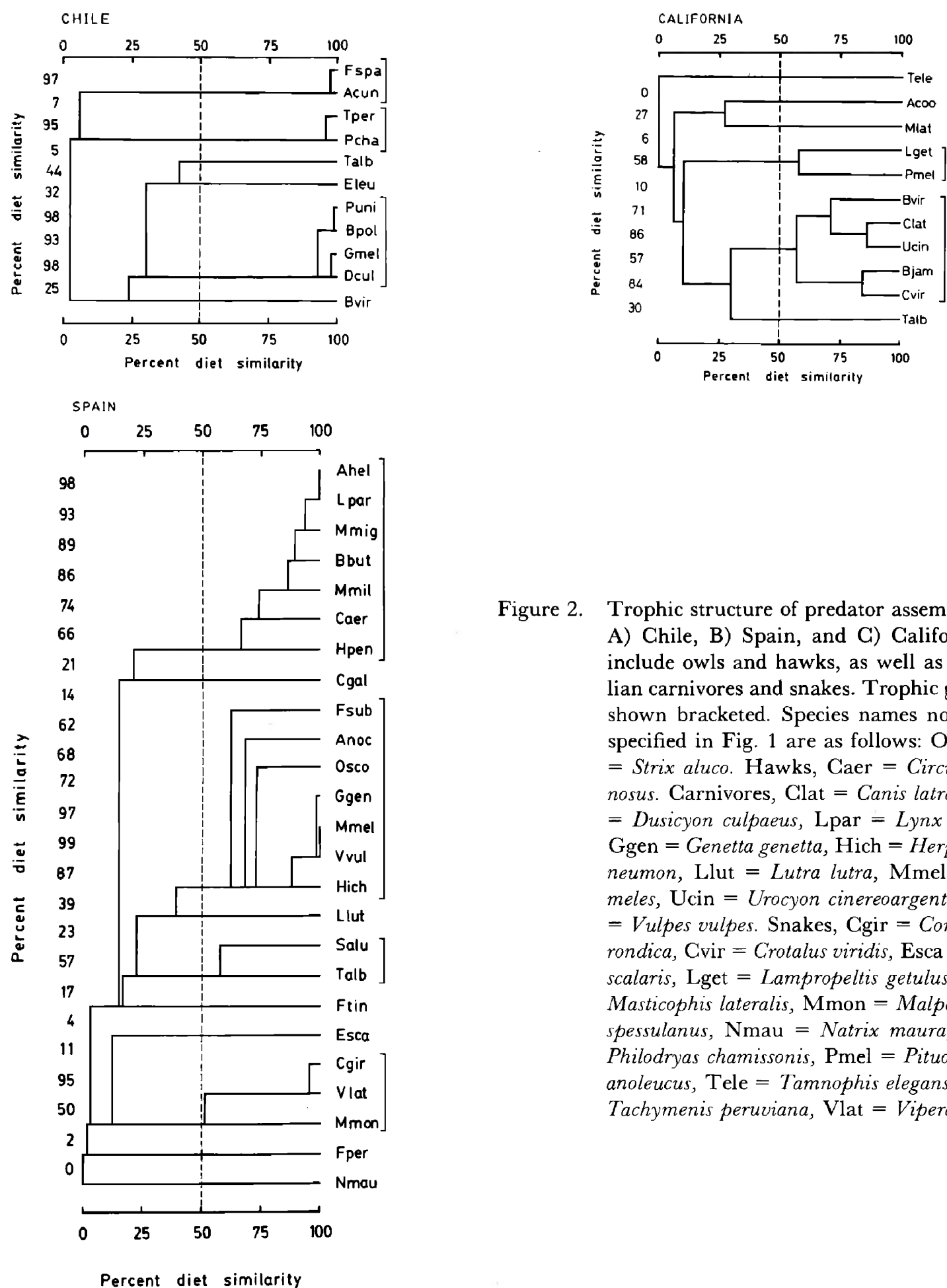


Figure 2. Trophic structure of predator assemblages in: A) Chile, B) Spain, and C) California that include owls and hawks, as well as mammalian carnivores and snakes. Trophic guilds are shown bracketed. Species names not already specified in Fig. 1 are as follows: Owls, Salu = *Strix aluco*. Hawks, Caer = *Circus aeruginosus*. Carnivores, Clat = *Canis latrans*, Dcul = *Dusicyon culpaeus*, Lpar = *Lynx pardinus*, Ggen = *Genetta genetta*, Hich = *Herpestes ichneumon*, Llut = *Lutra lutra*, Mmel = *Meles meles*, Ucin = *Urocyon cinereoargenteus*, Vvul = *Vulpes vulpes*. Snakes, Cgir = *Coronella girondica*, Cvir = *Crotalus viridis*, Esca = *Elaphe scalaris*, Lget = *Lampropeltis getulus*, Mlat = *Masticophis lateralis*, Mmon = *Malpolon monspessulanus*, Nmau = *Natrix maura*, Pcha = *Philodryas chamissonis*, Pmel = *Pituophis melanoleucus*, Tele = *Tamnophis elegans*, Tper = *Tachymenis peruviana*, Vlat = *Vipera latasti*.

ianus in Chile, California and Colorado and by *Bubo bubo* in Spain.

Trophic metrics computed plus mean weight of owls from different localities are presented in Table 1 for *Athene*, *Tyto* and *Bubo*. Diet breadths of the

four owl populations vary widely and inconsistently, with rank orders varying from site to site and showing clear crossovers (Fig. 4A). The same is observed in the case of the mean prey weights (Fig. 4B), as standardized by mean weight of corresponding owl

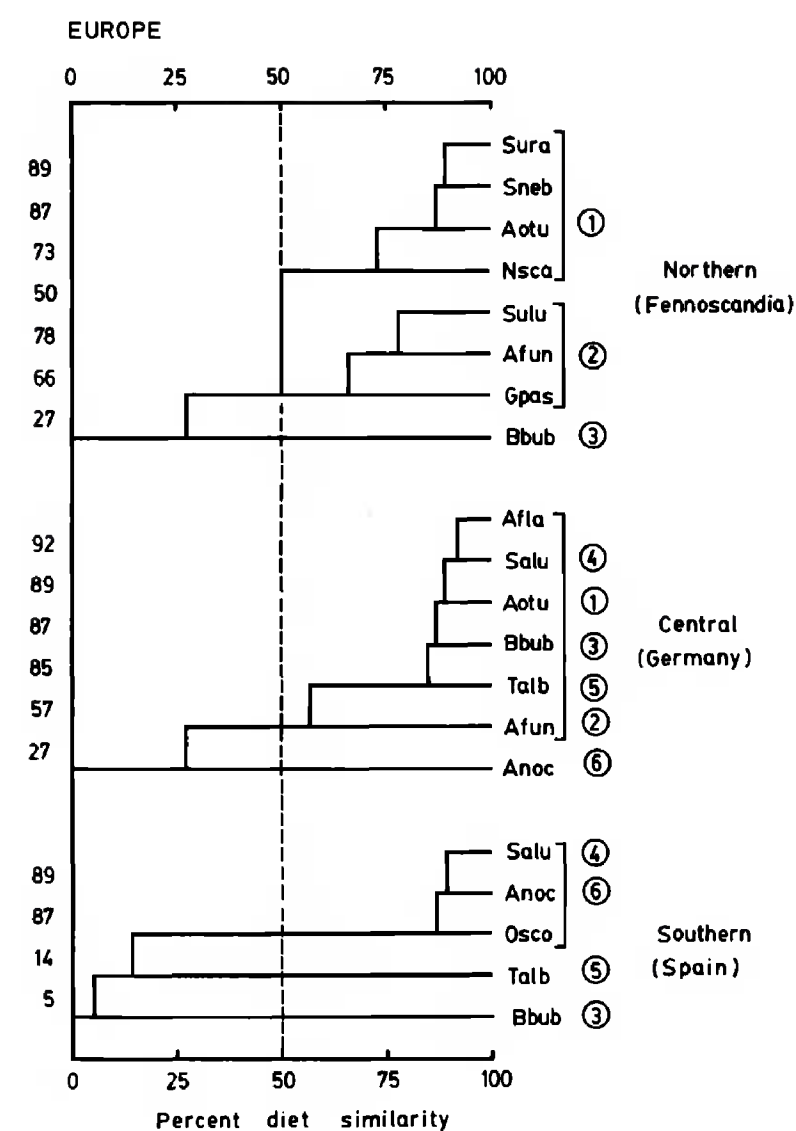


Figure 3. Trophic structure of owl assemblages in different regions of Europe (modified from Herrera and Hiraldo 1976). Trophic guilds are shown bracketed. A species that is present in more than one region is given the same serial number to aid in its localization. Names of owl species not already specified in Figs. 1 or 2 are as follows: Afun = *Aegolius funereus*, Bbub = *Bubo bubo*, Gpas = *Glaucidium passerinum*, Nsca = *Nyctea scandiaca*, Sneb = *Strix nebulosa*, Sura = *Strix uralensis*, Sulu = *Surnia ulula*.

populations. Notice that owls of different sizes vary markedly in relative prey weights, showing reversals and crossovers in rank orders.

These results suggest that each owl population responds individually, and perhaps opportunistically, to the local profile of prey sizes and abundances (see also Korschgen and Stuart 1972; Phelan and Robertson 1978; Korpimäki 1984, 1985a, 1985b, 1986a; Janes and Barss 1985; but see Nilsson 1984; Korpimäki 1987b; Korpimäki and Sulkava 1987, to the contrary). Further, owl populations seem to exploit prey resources with no regard for fixed optimal

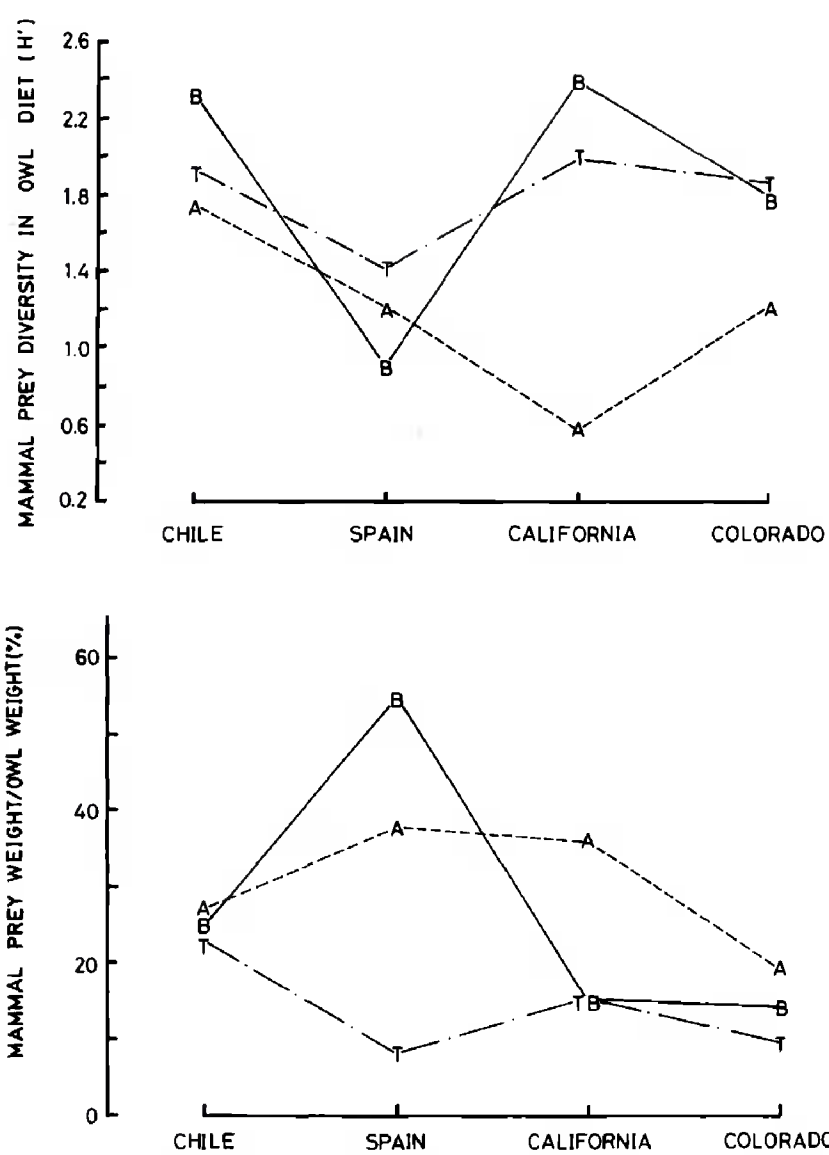


Figure 4. Trophic diversity (diversity of mammal prey in the diet), and relative prey weight expressed as percentage (weight of mammal prey in the diet relative to owl weight, as reported in Table 1) of owls in Chile, Spain, California, and Colorado. Symbols mean as follows: A = *Athene*, B = *Bubo*, T = *Tyto*.

prey size or diet breadth (see also Jakšić and Braker 1983; Janes and Barss 1985; Ekman 1986). Apparently, varying characteristics of trophic structure of owl assemblages emerge from idiosyncratic behavior within local owl populations.

DISCUSSION

Several theoretical and practical implications emerge. First, the significance of time as a niche axis for separation of owls and hawks cannot be sustained under the tenets of classic competition theory. Interference interactions between hawks and owls, rather than presumed exploitation competition, may be a major factor underlying their different activity times (see Jakšić 1982; Carothers and Jakšić 1984; Korpimäki 1987b). It should be interesting to explore why owls have not more thoroughly invaded

Table 1. Trophic metrics used to characterize congeneric owls in different localities. Trophic diversity was calculated at the species level of mammalian prey, and mean prey size also refers to mammalian prey only. Figures in parentheses are sample sizes; standard errors for mean prey size and mean owl size are provided in Jaksic and Marti (1981, 1984) and Jaksic et al. (1982).

TROPHIC METRICS				
SPECIES	CHILE	SPAIN	CALIFORNIA	COLORADO
Trophic diversity				
<i>Athene</i>	1.741 (503)	1.213 (8)	0.574 (896)	1.215 (388)
<i>Tyto</i>	1.932 (3417)	1.409 (12 492)	1.988 (7832)	1.856 (4305)
<i>Bubo</i>	2.314 (735)	0.897 (2281)	2.396 (2235)	1.803 (2141)
Mean prey size (g)				
<i>Athene</i>	67.3 (503)	56.0 (8)	55.2 (896)	29.0 (388)
<i>Tyto</i>	70.7 (3391)	21.2 (12 351)	68.2 (7827)	45.9 (4305)
<i>Bubo</i>	303.3 (660)	1037.9 (2277)	179.7 (2222)	207.1 (2141)
Mean owl size (g)				
<i>Athene</i>	247.0 (3)	148.0 (30)	154.0 (19)	150.5 (9)
<i>Tyto</i>	306.5 (8)	280.6 (20)	442.1 (15)	479.0 (?)
<i>Bubo</i>	1227.2 (6)	1885.5 (8)	1166.1 (30)	1460.3 (14)

the diurnal hunting period (indeed, *Asio flammeus*, *Athene* spp., *Glaucidium* spp., *Nyctea scandiaca*, *Strix aluco*, *S. nebulosa*, *S. varia* and *Surnia ulula* have made a partial transition to diurnality).

Secondly, temporal partitioning by owls (or other vertebrate predators) may not serve to reduce presumed resource exploitation but to minimize resource depression (see Charnov et al. 1976; Nilsson et al. 1982; Maurer 1984; Korpimäki 1987b): reduced availability of prey owing to their behavioral response to hunting predators. Although owls were not considered by Nilsson et al. (1982) to hunt for “evasive” prey such as birds and medium-sized mammals, I think the idea that owls may indeed depress their small mammal prey deserves testing. The role of different hunting modes as a means of alleviating resource depression deserves more attention (Jaksic 1985; Jaksic and Carothers 1985; Korpimäki 1986b). On the other hand, temporal partitioning may be an epiphenomenic response that serves to minimize frequency of agonistic encounters with aggressively dominant owls (Mikkola 1976; Jaksic 1982; Mikkola 1983), rather than a direct consequence of exploitation competition.

Thirdly, if habitat is only the arena in which owls dispute access to prey resources, perhaps habitat partitioning is also a means to minimize resource depression rather than presumed exploitation competition (see Maurer 1984). What would be the effect of removing dominant owls (e.g., *Bubo virginianus*, *B.*

bubo or *Strix uralensis*) on the abundance and diversity of local predator assemblages (see Rudolph 1978; Mikkola 1983; Korpimäki 1987a; for hints)? Why are there often fewer sympatric species of owls than hawks (Jaksic 1983)? What are the relative abundances of sympatric predators in the same guild? These questions deserve further research.

On the practical side, extrapolation of trophic characteristics of known owl populations is risky (even between comparable habitats), and the set of guild members is unpredictable (and often includes more than owls). Consequently, conservation/management measures should be based on field studies that include not only the target species but all potential guild members. Applied studies should consider that the intensity of ecological interactions among owls and with other predators is mediated not only by exploitation of shared prey, but perhaps more strongly by aggressive dominance.

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